



Climate-driven changes in functional biogeography of Arctic marine fish communities

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Climate change triggers poleward shifts in species distribution leading to changes in biogeography. In the marine environment, fish respond quickly to warming, causing community-wide reorganizations, which result in profound changes in ecosystem functioning. Functional biogeography provides a framework to address how ecosystem functioning may be affected by climate change over large spatial scales. However, there are few studies on functional biogeography in the marine environment, and none in the Arctic, where climate-driven changes are most rapid and extensive. We investigated the impact of climate warming on the functional biogeography of the Barents Sea, which is characterized by a sharp zoogeographic divide separating boreal from Arctic species. Our unique dataset covered 52 fish species, 15 functional traits, and 3,660 stations sampled during the recent warming period. We found that the functional traits characterizing Arctic fish communities, mainly composed of small-sized bottom-dwelling benthivores, are being rapidly replaced by traits of incoming boreal species, particularly the larger, longer lived, and more piscivorous species. The changes in functional traits detected in the Arctic can be predicted based on the characteristics of species expected to undergo quick poleward shifts in response to warming. These are the large, generalist, motile species, such as cod and haddock. We show how functional biogeography can provide important insights into the relationship between species composition, diversity, ecosystem functioning, and environmental drivers. This represents invaluable knowledge in a period when communities and ecosystems experience rapid climate-driven changes across biogeographical regions.

Barents Sea | climate warming | marine ecosystems | trait-based ecology | functional traits

Climate change triggers shifts in species distribution, affecting marine biogeography (1, 2). Particularly, the Arctic is experiencing some of the highest warming rates observed around the globe in recent decades (2, 3), leading to alterations in marine species composition (4, 5). The current change in Arctic marine biogeography is largely due to the poleward movement of boreal species following an increase in water temperature and loss of sea ice (5–7). The incoming boreal species differ markedly from Arctic species with regard to functional characteristics (8–10), and are thereby expected to strongly affect ecosystem functioning in the Arctic.

The implications of changing biogeographic patterns for ecosystem functioning can be addressed by the emerging field of functional biogeography (11). Functional biogeography integrates knowledge on patterns of species distribution with information on how species affect ecosystem functioning via an analysis of species' functional traits in large-scale, spatially explicit studies (11). This approach promotes our understanding of species' functional roles in the ecosystem along biogeographic gradients (12–14). Functional biogeography can thus be applied to address the ecosystem functioning effects of rapid and extensive climate-driven changes in biogeography (15–17), which are likely to initially involve species with functional characteristics such as high motility, broad niche, and high trophic level (4, 14, 18–20).

Studies of functional biogeography require detailed information on the distribution of species and their functional characteristics. To date, the assessment of variation in functional traits over biogeographic scales has been mostly limited to terrestrial organisms, such as plants (13, 21–24), mammals (12, 25–28), birds (29, 30), arthropods (31–33), parasites (ref. 34, also including freshwater species), and microbes (35), even though climate warming is affecting species distribution faster in the marine than in the terrestrial environment (36, 37). Unlike the terrestrial environment, the most important barriers to range expansion in marine systems, particularly for fish, are climatic rather than physical (38). This is especially important in the Arctic, where warming rates are highest (3, 39). Higher temperatures in the Arctic are reducing sea ice coverage, age, and thickness (40–42), which increases light availability favoring visual predators (43) and boosting pelagic primary production (44–47). These changes should contribute to the poleward range expansion of fish species with higher swimming ability, generalist resource use (14), affinity for warmer waters (36), and potential to exploit the increased pelagic production. Conversely, species with narrower diet breadth or at lower trophic levels are expected to respond more negatively to climate warming (4) due to lower dietary flexibility and higher predation rates.

Here we address the functional biogeography of Barents Sea fish during the recent period of rapid warming. There are indications of an ongoing borealization of the Barents Sea fish

Significance

Arctic marine ecosystems are experiencing a rapid biogeographic change following the highest warming rates observed around the globe in recent decades. Currently, there are no studies of how the observed shifts in species composition are affecting Arctic marine ecosystem functioning at a biogeographic scale. We address this issue via functional biogeography and show that increasing temperatures and reduced ice coverage are associated with the borealization of Arctic fish communities. We find that large body-sized piscivorous and semipelagic boreal species are replacing small-bodied benthivorous Arctic species, likely affecting biomass production in the benthic and pelagic compartments and their coupling. The documented speed and magnitude of climate-driven borealization will profoundly alter ecosystem functioning in the Arctic.

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community, where boreal species are expanding north and eastward, possibly replacing several of the more typical Arctic species (5). We assessed how variation in sea-bottom temperature and sea ice coverage is affecting the functional identity of the Arctic fish communities by using a unique dataset covering the entire Barents Sea over 9 y. Spatial patterns and temporal trends in functional traits of fish species are addressed at the community level using an approach that characterizes the functional identity of communities based on multiple traits. We hypothesized that, in the Arctic region, climate warming would favor the expansion of traits typical of boreal species, such as generalism and large body size, and lead to a reduced prevalence of fish traits related to benthivory, which is typical of Arctic communities.

Materials and Methods

Study Area. The Barents Sea is a shallow shelf sea (average depth 230 m) of 1.6 million km² extending from northern Norway to the Svalbard archipelago (at 80° N), and from the shelf edge (5–8° E) in the west to Franz Joseph Land and Novaya Zemlya archipelagos in the east. The region is influenced by the Atlantic Water (bottom temperature >2 °C, salinity >35‰) and the Arctic Water (bottom temperature <0 °C, salinity between 34.4 and 34.7‰). The polar front separates the boreal and Arctic faunal assemblages in a zone of mixed-water masses (48). The Atlantic Water maintains a high pelagic productivity. In contrast, the colder Arctic Water is lower in nutrients and pelagic productivity, but has higher megabenthic secondary production (49). The Barents Sea has experienced an increase in average water temperature over the past decades due to an increased inflow of Atlantic Water northwards and a reduction in sea ice coverage (3, 6, 7). Among the most common fish species found in the Barents Sea, cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) dominate the boreal community, whereas sculpins (*Ictalus* spp. and *Triglops* spp.), snailfish (*Liparis* spp.), and Greenland halibut (*Reinhardtius hipoglossoides*) dominate the Arctic community (5, 48).

Sampling Procedure. Fish abundance data were obtained from the Barents Sea ecosystem survey, a cooperation between the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Russia and the Institute of Marine Research (IMR) in Norway. A shrimp bottom trawl (Campelen 1800) was towed at ~3 kn for 15 min. As a rule, stations were allocated on a standardized grid (35 nautical miles between stations) across the Barents Sea shelf, resulting in ~350 sampling stations every year (48, 50). Here, we report data from the start of the ecosystem survey in 2004 until 2012, for a total of 3,660 sampling stations.

Species Selection and Functional Traits. Reliable and comprehensive information on fish functional traits (8, 9, 51) was available for 52 of the 74 fish taxa reported in Fossheim et al. (5), and these were included in the present work (Table S1). The 52 species accounted for 99.6% of all demersal fish individuals collected in the surveys.

We characterized each of the 52 fish species using information on functional traits related to different aspects of fish biology and ecology. The chosen traits contained information on (i) life history, (ii) body size, (iii) feeding ecology, (iv) habitat affinity, and (v) food web position (Table S2). Body size, feeding ecology, habitat affinity, and food web-derived traits can be defined as effect traits (52), because they can be directly linked to their effects on ecosystem functioning. The ecosystem function interpretation of our traits is given by Wiedmann et al. (8), with the exception of the food web-derived traits that were obtained using information from a highly resolved Barents Sea food web (10, 51).

Life-history traits included maximum age, mean fecundity, average egg size, and growth rate. The latter was calculated as the ratio between mean size at maturation and mean age at maturation. Maximum body length was used as a measure of body size. Feeding ecology was derived from information on the most common food items in the diet, and was categorized into benthivorous, planktivorous, and piscivorous diet. Although most species sampled in this study are typically demersal, some can be classified as semipelagic, because they may use the pelagic compartment for feeding, such as cod and haddock. Thus, we further characterized species by their affinity to the two habitats as demersal or semipelagic. Food web-related traits included number of feeding links to prey taxa (in-degree), number of links to predator taxa (out-degree), and information on the potential degree of omnivory of the species (10). A more generalist diet, i.e., high in-degree, implies the use of a higher variety of energy sources. Similarly, a species with a greater number of links to predators, high out-degree, is a source of energy for many species. The

degree of omnivory of a consumer is measured as the variability in trophic level among the trophospecies included in its diet (53) and provides information on the energy flow in the ecosystem. Body size, growth rate, and the food web metrics were coded as continuous variables, whereas for the remaining traits we relied on fuzzy coding (54).

Environmental Drivers. Along with information on fish species composition, the ecosystem surveys also collected on-site data on bottom water temperature, salinity, and depth. Bottom water temperature, ice coverage, and depth are important descriptors of habitat conditions, whereas salinity indicates the prevalence of the different water masses, Arctic or Atlantic, at each station (5, 55, 56). Information on ice coverage was obtained from satellite images (57) and is reported here as the number of days a location was covered with ice during each year.

Data Analysis. To assess how the individual species were characterized in terms of their traits, we first analyzed the trait by species matrix via principal component analysis (PCA). Before analysis, the functional traits were centered and standardized to unit SD to limit the effect of scale on the PCA outcome. To assess how the sampling stations were characterized in terms of their traits, we computed mean functional trait values at the community level by weighting the traits by the abundance of all species sharing them at a given sampling station, following the community-weighted mean trait value (CWM) approach (58). The approach assumes that the effect of functional traits on the ecosystem depends on the abundance of individuals carrying those traits. The resulting 3,660-station by 15-trait CWM matrix was analyzed using PCA, scaling the data as indicated above. We used the first principal component axis (PC1), which accounts for most of the variation in the data, as our indicator of functional characterization at the community level for each station (CWM PC1) (e.g., ref. 59). Including data for all years in the CWM PCA allowed us to address variation in the CWM characterization of sampling stations across years. The analyses of functional characterization were performed in R (60) and relied on the R package *FD* (61).

To assess how trait composition at the community level has changed over time in specific zoogeographic regions, we subsampled the Barents Sea data in two contrasting regions, Arctic and boreal, previously defined by Fossheim et al. (5) and Kortsch et al. (10). For each region, we calculated the mean value of the CWM PC1 and the mean CWM for each individual trait across all sampling stations. We analyzed region-specific temporal trends in community-weighted functional traits using linear regressions, and we included the interaction term between year and region, without accounting for possible temporal autocorrelation. When the interaction between year and region was significant, visual inspection of the trends indicated whether the CWM trait values converged or diverged over time.

We then identified the main abiotic drivers of change (bottom water temperature, salinity, depth, and number of days with sea ice coverage) in CWM PC1 by using random forest analysis (62). Random forest analysis, a machine-learning technique that uses a combination of regression trees, evaluates which predictor variables are the most important in accounting for the variation in the data. Variable importance is assessed based on changes in the mean square error (MSE) of the model compared with a model on permuted data, where a higher percentage increase of MSE (%IncMSE) indicates a higher importance of that variable. To generate an overview of how the environmental variables might affect the functional identity of communities, we first ran a random forest analysis on all 9 y of the study pooled together. Because the importance of each environmental variable across years is expected to vary, we also constructed random forests for each year. Regression trees for each year were used to estimate the environmental threshold values that best describe variation in CWM PC1. Threshold values are obtained by successively partitioning the predictor variables into two groups according to the variation explained in the response variable. Random forests and regression tree analyses were performed in R using the packages *randomForest* (62) and *tree* (63), respectively.

The influence of the abiotic drivers on CWM PC1 variation was further investigated by spatial modeling using generalized mixed-effect models with an explicit spatial autocorrelation structure of order 1 (corCAR1) that included longitude and latitude as covariates. The response variable varied nonlinearly with temperature, which was thereby included as a quadratic term in the model. Years were specified as random slopes to account for between-year differences in the relationship between the abiotic variables and CWM PC1. We used the R packages *nlme* (64) for fitting the model and *piecewiseSEM* (65) for assessing the marginal and conditional *r*² values (66).

Results

Functional Characteristics of Fish Species. Our PCA on fish species functional traits indicated that most species in our study are benthivorous, have high affinity to the demersal compartment, a relatively small body size, slow growth rate, and few feeding links to both prey and predators (Fig. S1). Species with those traits have relatively low abundance and are found more frequently in the northernmost regions of the Barents Sea (67). Recent work has indicated that these traits often characterize Arctic benthic fish communities (5, 9) and are hereafter named Arctic-like traits for simplicity. Examples of species groups with these characteristics are sculpins and snailfish. In contrast, the most abundant species found in the ecosystem surveys are piscivorous with higher affinity to the pelagic compartment, have higher number of food web links to both predators and prey, are more omnivorous, and have higher growth rate and larger body size (Fig. S1). This configuration of traits is most clearly expressed in cod, but is also found in redfish (*Sebastes mentella*) and haddock. Species carrying those traits have their main occurrence in the southwestern and central regions of the Barents Sea (67). These traits are more typical of North Atlantic boreal communities (9, 10, 55) and are hereafter termed boreal-like traits.

Community-Weighted Mean Trait Values. PC1 accounted for 60% of the variation in CWM data (Fig. S2) and was used as the indicator of the functional characteristics—i.e., the functional identity—of the fish communities in the Barents Sea. The PC1 left-hand side indicated that stations characterized by species with many food web links to predators also had many food web links to prey. These high-degree centralities indicate higher trophic connectivity in these communities. Communities of fish with many feeding links were characterized by higher affinity to the pelagic compartment and greater reliance on a fish diet. A more pronounced degree of omnivory was also a characteristic of these communities. Finally, fish species in these communities had large body size and higher growth rate. On the right-hand side of PC1 were communities characterized by benthivory and higher affinity to the demersal compartment, with fewer food web links to prey and predators, smaller size, and lower growth rate. The second principal component (PC2) captured ~19% of

the variance in the CWM data and was associated with habitat and feeding preferences.

Spatiotemporal Distribution of Mean Trait Values. Across all years, the northeastern Barents Sea was dominated by Arctic-like traits consisting of benthivorous diet, small body size, lower fecundity, and few food web links. The southwestern region of the Barents Sea was dominated by boreal-like traits, which differed markedly from the above trait configuration, with pelagic diets, large body size, high fecundity, and many feeding links (Fig. 1 and Fig. S3 for all years).

In 2004, the Arctic-like traits were dominant traits in an area covering nearly 50% of the Barents Sea, and by 2012 those communities covered less than 20% of the Barents Sea (Fig. 1). An area of mixed traits, where the dominant trait was neither boreal-like nor Arctic-like was seen across all years in the central region, roughly corresponding to the mixed-water region. The total area covered by these mixed traits reached its peak in 2007, after increasing from 2004 to 2006. Sampling stations dominated by boreal-like traits also increased in frequency from 2004 to 2012 (Fig. S3).

There was a convergence of Arctic communities toward boreal-like communities from 2004 to 2012, exemplified by the increase in piscivory, fecundity, development rate, and use of the pelagic compartment in the Arctic region (region by time interactions: $P < 0.05$; Fig. 2 and Fig. S4 and Table S3 for all traits). The boreal region mostly maintained or even increased the dominance of boreal-like traits throughout the study period (Fig. 2 and Fig. S4 and Table S3).

Environmental Effects on Trait Identity. The random forest analysis of all 9 y of sampling explained 48.5% of the variance in CWM PC1. Days of ice coverage and water temperature were the two most important predictors, followed by salinity and depth. The main environmental thresholds changed from sea ice to water temperature over time, possibly as a consequence of sea ice retraction, which reduced the scope for strong associations between sea ice and CWM PC1 (Fig. 3 for 2004 and 2012; Figs. S5 and S6 for all years).

Our regression trees confirmed that sea bottom temperature and ice coverage were the most important environmental variables explaining variation in CWM PC1. In the first year of

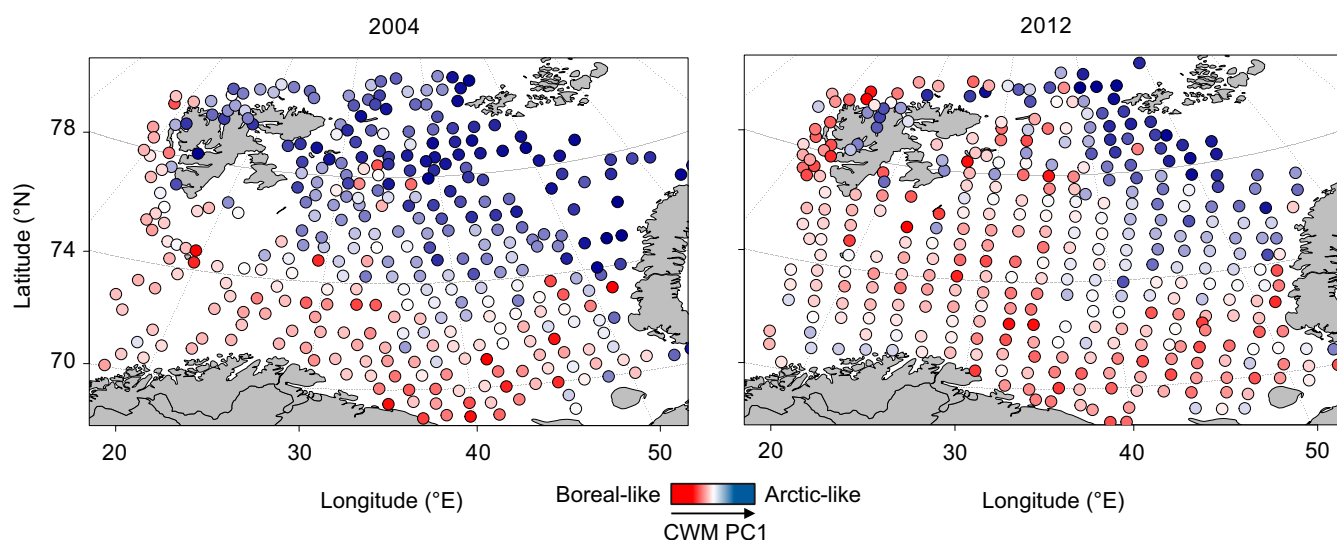


Fig. 1. Spatial distribution of functional traits in the Barents Sea fish communities in 2004 and 2012. Colors indicate the dominant trait characteristics of each community as obtained from PC1 of abundance-weighted trait values and range from red (boreal-like) to blue (Arctic-like). Boreal-like trait values indicate communities dominated by large body-sized, generalist, piscivorous, and semipelagic species. Arctic-like trait values indicate dominance of small body-sized, benthivorous, and more strictly demersal species.

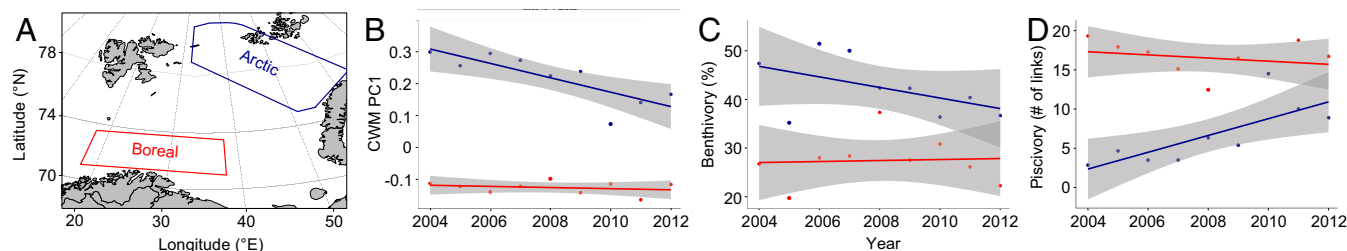


Fig. 2. (A) Boreal (red) and Arctic (blue) regions used for assessing trends (from 2004 to 2012) in (B) CWM trait values for all traits (PC1), (C) benthivory, and (D) piscivory (see Fig. S4 for all traits). Data points are the average within each region, and the trend lines are estimated by linear regression. The 95% confidence bands are shown in gray.

sampling, 2004, ice was the most important predictor, with a threshold value of 57 d with ice coverage (Fig. 3). Sampling stations below that threshold were mostly characterized as boreal-like communities when water temperature was above 0.51 °C at the time of sampling, and as Arctic-like communities when water temperature was below 0.51 °C. Sampling stations with more than 57 d with ice coverage were mostly characterized as Arctic-like communities. In 2012, the last year of sampling, temperature, but not ice, was the main predictor of variation in CWM PC1 (Fig. 3). Sampling stations were mostly characterized as Arctic-like at water temperature below 1 °C, and as boreal-like above that threshold. A secondary threshold, days with ice coverage, further explained the variation in CWM PC1 below and above that first threshold. The number of sampling stations characterized as Arctic-like decreased from 2004 to 2012 (Fig. 3).

When pooling the data across the entire Barents Sea for all years our mixed-effect model indicated that bottom water temperature, salinity, days with ice coverage, and depth are all related to changes in CWM PC1 (all $F > 16.04$, $P < 0.001$. Marginal $r^2 = 0.40$; conditional $r^2 = 0.46$). In summary, waters that are warmer, more saline, shallower, and have fewer days with ice coverage have fish communities dominated by boreal-like traits (Fig. S7).

Discussion

We found large differences in trait characterization between the boreal and Arctic communities of the Barents Sea. This difference is consistent with the zoogeographic distribution of fish species (5, 48) and is related to the Arctic and Atlantic water masses distribution in the region. Functional trait distribution changed rapidly, especially in the Arctic, concurrent with the observed increase in sea bottom temperature and reduction in

sea ice coverage. The borealization of functional traits in the Arctic has profound consequences for the functioning of this marine ecosystem. The movement of large-bodied generalist species has the potential to reconfigure the Arctic food webs (10) and affect ecosystem functioning in the region.

Functional Biogeography. The difference in trait composition between Arctic and boreal regions reflects strong differences in resource use and habitat affinities. Larger species and species with higher growth rate, typical of boreal communities, require more food to maintain growth. Boreal communities are more dependent on the pelagic phytoplankton production (68) than Arctic communities. Additionally, the more generalist and omnivorous feeding types among the boreal species suggest the use of a broader resource spectrum and a greater potential to exploit and affect diverse prey across the food web. Fish species with these characteristics can have a considerable impact on food web connectance (10). Moreover, they enhance other types of food web configurations such as loops, where one large generalist species may feed on its own predator, with consequences for energy flow in the system. Due to their large body size and high trophic level, these fish may have a strong regulating role via top-down effects (69, 70).

In contrast to the boreal region, the colder and more nutrient-depleted Arctic region of the Barents Sea is characterized by lower consumption and higher reliance on benthivory. The seasonal sea ice coverage and low water temperatures influence these characteristics. Under the sea ice, a small zooplankton community feeds on ice algae supporting many of the pelagic species (71). A large fraction of this production is not consumed in the pelagic compartment, but sinks to the bottom, fueling benthic secondary production (49, 56, 72). Thus, with the exception of very few

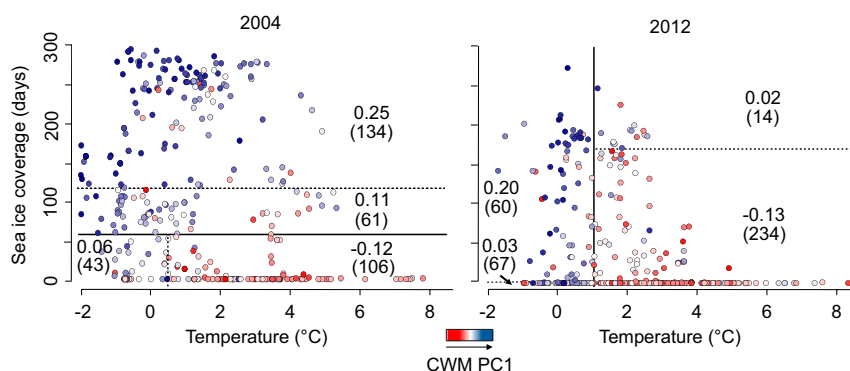


Fig. 3. Distribution of fish functional traits in the Barents Sea along two environmental variables affected by warming in 2004 and 2012. Colors code the dominant trait characteristics from red (boreal-like) to blue (Arctic-like) as in Fig. 1. The two environmental variables displayed were the most important explanatory variables in the regression tree analyses. Lines indicate the threshold values for the environmental variables obtained by the regression tree (solid lines, first threshold values; dotted lines, second threshold values). Numbers indicate the mean CWM PC1 value (and number of stations) for stations found within ranges of environmental characteristics specified by the environmental threshold values.

pelagic fish species (e.g., polar cod, *Boreogadus saida*), most fish species in the Arctic are typically demersal and benthivorous specialists (73). Their small body size and low growth rate indicate low resource requirements.

Climate-Driven Change in Functional Composition. We found a dramatic shift in functional trait composition in the Arctic region of the Barents Sea from 2004 to 2012. This is the region where the largest climate-driven changes in fish community structure have been observed (5). The prevalence of functional traits typical of the boreal communities is increasing rapidly in the Arctic region. These functional traits are related to large body size, piscivory, a high exploitation of pelagic prey, high generalism, and omnivory. The increased dominance of boreal-like traits is particularly pronounced around Svalbard.

One key factor that may help explain the shifts in trait distribution is linked to the sea ice retraction observed in the Barents Sea over the past decades. This retraction in sea ice increases light availability in the region (43) due to reductions in both ice thickness and sea ice-covered area. The resulting longer open water season in the Arctic has a positive effect on pelagic net primary production (46, 74) and potentially leads to the development of a novel phytoplankton bloom in autumn (45). In the last two decades, primary production increased in the region where the Atlantic and Arctic water masses meet (74), and where a poleward expansion of boreal fish species has been observed in recent years (5). Whereas sea ice retraction positively affects the poleward expansion of boreal-like traits, it negatively affects the prevalence of Arctic-like traits. This may be caused by a continuous ice retraction that affects habitat characteristics necessary for many Arctic species (4). The change from sea ice algal production to the new spring algal bloom may cause a mismatch in timing between primary producers and herbivores and can be a strong limiting factor for the adaptability of some Arctic fish species (46). The reproductive strategy of many Arctic fish species is also linked to the melting of sea ice and the subsequent high primary and secondary production (75). Finally, the Atlantic Water may reach a temperature above the thermal capacity of several Arctic species while being suitable for the boreal ones (76). These Arctic species are hindered from moving further northwards because they are limited by the edge of the sea shelf (71). Preliminary results for the Barents Sea fish data collected following 2012 are consistent with the trends documented in our study (67, 77); thus it is possible that Arctic fish species will go locally extinct in the Barents Sea as the water temperature continues to rise and sea ice retreats.

The Arctic region of the Barents Sea displayed the largest shift in functional identity, as boreal-like traits became more common and started dominating the demersal fish communities. This region has also experienced the highest variation in functional diversity across recent years, from relatively low values in 2004 and 2005 to relatively high values in 2007 and 2008 (8). Our results indicate that the increased functional diversity in the Arctic observed by Wiedmann et al. (8) is due to the addition of

boreal-like traits, and not to an increase in the local diversity of Arctic species.

Ecosystem-Level Implications of the New Trait Composition in the Arctic. Our results indicate important effects of climate warming on ecosystem functioning in the Arctic region of the Barents Sea. Although we did not measure ecological processes linked to functioning directly, some predictions are possible. For example, the current decrease in benthivorous fish observed in the Arctic Barents Sea may decrease the coupling between pelagic and benthic compartments driven by semipelagic and pelagic piscivorous fish. This reduction in benthivorous fish will likely affect benthic secondary production (49), which is currently the most important resource sustaining the Arctic fish community.

The observed increase in body size, generalist diet, and omnivory in the Arctic fish communities indicates a higher consumption rate and higher energy flow across the whole food web. The higher consumption rates of large omnivorous species that have newly entered the Arctic region will likely reduce the biomass of smaller Arctic species, which have generally low fecundity. These Arctic species may even be eliminated from the region, with negative consequences for production at high latitudes during the long polar winter. Similar ecosystem-level effects are expected in other Arctic seas, such as the Bering Sea, where the trophic level of commercial fisheries has increased with increasing temperature and decreasing sea ice extent (4).

Climate Change and Functional Biogeography. Despite the rapid change in species composition and distribution observed across the globe due to climate warming (17), little is known about its implications for ecosystem functioning at large spatial scales. The rates of change may be highest at high latitudes, where the highest rates of increase in temperature are observed and expected (3), but climate change impact on functional biogeography can be expected across the globe in all ecosystems. By looking at the distribution of functional traits, general hypotheses on climate-trait relationships can be extrapolated from our results to other marine, terrestrial, and freshwater ecosystems. One general expectation is the addition of motile, larger body-sized, generalist species to higher latitudes. The magnitude of the effects will depend on the difference in functional characteristics between adjacent biogeographic regions. However, whether climate change triggers distributional shifts in functional traits at the global scale is to date uncertain given the paucity of studies linking traits to biogeography in changing environments.

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